

14.—Physiology of the Quokka

Investigations of physiological processes operating in the quokka have been carried out during the last 10 years by a number of people in various capacities and of different interests. As a result, these studies have not followed a systematic sequence but are linked by the common interest of the investigators in the marsupial group. Therefore, rather than give a chronological account of the work done on the quokka, the following summary uses broad headings which group together investigations of related physiological processes.

Digestion

Few animals and no mammals form their own alimentary cellulase to digest the cellulose which encases plant cells. Consequently, those mammals which use plant material as food rely on unicellular organisms, which live in the digestive tract, to digest the cellulose portion of their food so that this substance can be made available for the animals' needs. This is particularly important in the case of grazing herbivores. Mammals can be divided into two groups by the manner in which micro-organisms assist them in this respect: the ruminants, in which the stomach is divided into four pouches, the first of these (the rumen) being the major site of predigestion of food by micro-organisms, and the non-ruminants, in which the stomach is a single compartment, digestive micro-organisms being contained in a relatively large caecum and in the colon.

The quokka, like other macropods, is an herbivorous animal of grazing habit. Moir, Somers, Sharman and Waring (1954), and Moir, Somers and Waring (1956) showed that in this animal the problem of digesting plant material is largely overcome by a type of "pregastric digestion" which is similar, in many respects, to that which occurs in ruminants. Thus, the stomach is large and sacculated, has an oesophageal groove and the proximal pouch contains bacteria which attack and ferment the food. As in ruminants, this bacterial results in production of volatile fatty acids which are absorbed mainly from the fore-stomach. However, the stomach of the quokka does not exactly resemble that of the ruminant; it is not known if the oesophageal groove functions as in ruminants and the functions of the distal pouches of the quokka stomach are unknown.

Two related characteristics of digestion in ruminants are the slow rate of passage of food through the alimentary canal and the small proportion of fibrous food that remains undigested. In investigating these processes in the quokka, Calaby (1958) observed that the rate of passage of food through the digestive tract in this animal is faster than in the ruminant but slower than in the horse; also that the percentage of dry food digested by the quokka is less than in ruminants but greater than in rabbits. Thus, digestion of plant material in the quokka is less efficient than in the domestic ruminant although probably more efficient than in non-ruminant herbivores.

Little is known of the essential food requirements of the quokka. In nitrogen balance trials, using a mixture of equal parts of oaten and

lucerne chaff and ground sheep nuts, J. H. Calaby (personal communication) obtained a preliminary figure for crude protein requirements for maintenance of adult animals, of approximately 3.5 grams per kilogram live body weight per day. Further information on this subject awaits future investigation.

Metabolism

General

The trend towards the specialised ruminant type shown by studies on digestion in the quokka are paralleled by some aspects of the metabolism of this animal.

Moir *et al.* (1954, 1956) recorded that blood volatile fatty acid (V.F.A.) and glucose levels in the quokka are similar to those found in ruminants, V.F.A. levels being higher and glucose levels lower than those normally found in non-ruminants; also V.F.A. was shown to be removed from the circulation by the liver and other tissues. These facts indicate that quokka tissues may be like those of the ruminant in utilising relatively large amounts of V.F.A. as an energy source. However the relative importance of V.F.A. and glucose in this respect are not yet known.

Further studies by J. Barker (unpublished) have shown that while normal blood glucose values for the quokka are similar to those for ruminants, feeding increases the blood glucose level to a rather greater extent than occurs in ruminants. However, intravenous injections of insulin in the quokka depress the blood glucose to very low levels which would not be tolerated by non-ruminants, this without apparent effect on the animal. This response is similar to that which occurs in ruminants. On the other hand, glucose tolerance times for the quokka are similar to those for non-ruminants and much shorter than those for ruminants. Finally, the ability of the quokka to convert injected propionate to glucose is considerably less than that of the ruminant although relatively greater than that of the rabbit.

Thus, although the quokka is like the ruminants in that it tolerates blood levels of V.F.A. and glucose that would not be tolerated by non-ruminants, some aspects of cell metabolism in this animal must differ from that of the ruminant, and full investigation of intermediary metabolism in the quokka should be of great interest.

Trace Elements

Cobalt and Copper.—Ruminants require cobalt for the synthesis of Vitamin B₁₂ by micro-organisms in the rumen. A higher intake level of cobalt is necessary in ruminants than in non-ruminants due to their poor faculty for absorption of Vitamin B₁₂ and to their requirement of a high level of cobalt in the rumen liquor to maintain a normal population of micro-organisms. In cobalt deficiency, rumen levels of cobalt are depressed. As a result, changes occur in the population structure of the resident micro-organisms and Vitamin B₁₂ production falls below the minimal requirements of the host. Thus the need for cobalt in ruminants is indirect and cobalt deficiency is in fact a defi-

ciency of Vitamin B₁₂. Ruminants become cobalt deficient when grazing light land low in cobalt and particularly when grazing coastal sand dune country consisting largely of wind born shell fragments.

After Moir *et al.* showed that the quokka had "ruminant-like" digestion, it was of interest to determine whether cobalt deficiency plays a part in limiting the numbers of quokkas on Rottnest Island, an area which consists entirely of sand dune formations and which has, in the past, proved an unsuitable area for grazing sheep. S. Barker (unpublished data) has attempted to produce experimental cobalt deficiency in quokkas. The basic diet used had a cobalt level of 0.02 p.p.m. (dry weight basis). This level is slightly lower than those found in the few Rottnest plants that have been analysed for cobalt. Although the liver cobalt levels in the quokkas were, after several months, significantly lower than those of control animals, serum levels of Vitamin B₁₂ did not approach the lowest levels found by Shield (1958) in the Rottnest population during spring months. No symptoms comparable with those exhibited by Vitamin B₁₂ deficient sheep were produced in quokkas on these low cobalt intake levels. It is therefore tentatively concluded that the quokka is more efficient than ruminants with respect to conversion of cobalt to Vitamin B₁₂ and/or to absorption of Vitamin B₁₂.

Copper deficiency occurs in ruminants under two types of circumstance—

- (1) a simple deficiency occurring in animals grazing on copper deficient pastures; and
- (2) an induced deficiency occurring in animals grazing pastures with normal copper levels but also with high molybdenum and inorganic sulphate levels—in this case an interaction between these three ions reduces the availability of copper to the animal.

By analysis of plants eaten by the quokka, S. Barker (unpublished data) has shown that Rottnest pastures are low in copper—the mean level being less than 5.0 p.p.m. (dry weight basis)—but field studies indicate that this in itself is adequate for the quokka. Also, in certain areas of the island, plants have a high molybdenum and inorganic sulphate content, and field studies have shown that during the summer, blood copper levels of animals in these areas fall below the winter levels. It therefore appears that when local population numbers build up during the summer, reduction in blood copper occurs in animals eating plants of high molybdenum and inorganic sulphate content. Preliminary experiments have indicated that a Cu-Mo-SO₄ interaction does exist in the quokka and further work on this problem is in progress.

Iron.—The mechanism of iron transfer from the female quokka to the suckling joey is being investigated by Kaldor. In eutherian mammals that have been studied, uterine embryos obtain iron for haemoglobin manufacture and iron storage as a result of placental transfer and such animals are born with a relatively high blood haemoglobin concentration. After birth the young are, for a time, dependent on the maternal milk for further iron supplies but eutherian milk has a low iron content. There-

fore, the young are largely dependent on their own iron stores during the lactation period and as these are not fully adequate for their needs, a characteristic decline in blood haemoglobin and in iron stores of the young occurs during this period. Blood haemoglobin and iron stores do not rise again until foods other than milk are taken.

Preliminary studies on the quokka have shown that the blood haemoglobin concentration is low in the young joey but rises throughout pouch life and towards the end of this period it is almost as high as the adult value. Storage iron in the liver is maintained at a constant high concentration during the corresponding period. These findings indicate an unusually high concentration of iron in quokka milk and this was confirmed by analysis. How this high output of iron in milk is maintained is the subject of work in progress as this is of great theoretical interest since there is no known mechanism for active secretion of iron into milk.

Water

Since Rottnest Island is an area where summer conditions are fairly prolonged and are coincident with a limited natural water supply, the quokkas living on the island might be expected to have some means of physiological adjustment to varied water availability.

Bentley (1955) described the ability of the quokka to concentrate its urine so as to maintain a positive water balance when drinking salt solutions as concentrated as 2.5% NaCl. However, most of his animals were not able to maintain a positive water balance when drinking sea water (equivalent to 3.3% NaCl). Therefore, animals living on Rottnest Island should be able to satisfy their summer water requirements by drinking any available brackish water, but while they may occasionally drink sea water, it is unlikely that they could survive over long periods with no other source of water. This is borne out by Bentley's field observations: urine samples collected from animals on the island during the winter were dilute while those collected during the summer were more concentrated, but the degree of concentration of summer field samples did not indicate any severe dehydration or show electrolyte concentrations that would indicate that the animals were drinking strong salt solutions. Therefore, animals which survive the summer are able to obtain sufficient water from their food and available fresh or brackish drinking water to maintain a positive water balance.

The structure of the quokka kidney was also described by Bentley and his observations indicated that the relative volume of reabsorptive tubule tissue exceeds the normal value for most other species. This may have physiological significance in relation to the wide seasonal variation in kidney secretory function observed in quokkas living in their natural habitat.

The possibility has been envisaged that if some seasonal fluctuation in the state of hydration of island animals does occur, this might be demonstrated by measurement of total blood volume at different times of the year. Preliminary work to test this was done by Ho (1958) and further work is being carried out by Shield

and Woolley, but no definite information regarding seasonal changes is yet available. The method used to assess total blood volume is the Evan's Blue (T1824) Dye method. Ho found that the time for complete mixing of injected dye in the circulation of quokkas is longer than is usual for other mammals and that the plasma volume per kilogram body weight is lower in the quokka (as in other marsupials that have been tested) than in eutherian mammals.

Temperature Regulation

Another important aspect of quokka physiology in relation to their environmental conditions is that of temperature regulation. Homiothermy is a general feature of eutherian mammals and is largely attained by evaporation of water from the skin and/or lung surfaces in hot ambient conditions, and by peripheral vasoconstriction and shivering in cold conditions. It was at one time thought that many marsupials, including the quokka, were not able to maintain a constant body temperature under conditions of gross changes in environmental temperature. That this is not true of the quokka has been clearly shown by Bentley (1955) and Bartholomew (1956) who observed very efficient homiothermy in quokkas subjected to high and low environmental temperatures.

Under hot conditions, the animals' respiration rates rose considerably, and Bentley observed that these increases were of the same order as those that occur in eutherian mammals of similar size such as the cat and the rabbit. He also described considerable sweating from the fore and hind paws, which he showed to be the only skin areas containing sweat glands. Both workers also described obvious salivation of quokkas in hot conditions and Bartholomew considered that evaporation of saliva, which the animals spread over their limbs and tail as a result of a "licking response to heat stress," was the major cooling factor. However, it is difficult to distinguish the relative roles of sweat and saliva in this respect since the behavioural licking response would spread both sweat and saliva to increase cooling by surface evaporation. Bentley (unpublished data) has shown that the licking response to heat stress is not essential for maintenance of the homiothermy exhibited by these animals, by using circular perspex collars that extended out from the neck, to prevent licking. Under hot environmental conditions, collared quokkas showed no increase of body temperatures compared to quokkas without collars; the paws became soaked with sweat which spread up the limbs and evaporation of this, together with the increased respiration rate, provided adequate cooling for the animals. It thus seems likely that the adjustable methods for heat loss in the quokka under natural conditions are largely a combination of panting and evaporation of sweat and saliva from parts of the body. These effects are enhanced by the behavioural pattern of licking. The licking response is acquired early in life (it was observed by Bartholomew in pouch young) and this worker also showed that homiothermy develops in the quokka during pouch life.

Bartholomew demonstrated that furred quokkas are also able to maintain their deep body temperature at normal levels when subjected to cold conditions with ambient temperatures as low as -10°C . This ability was accompanied by shivering and widespread peripheral vasoconstriction.

No data are available on metabolic rate changes in quokkas under hot or cold conditions.

Blood

Blood Groups

Blood group systems have been demonstrated in several mammalian species and provide interesting material for genetical studies. An investigation of naturally occurring blood group antigens and antibodies in the quokka was carried out by Saunders (1958). The preliminary findings indicate that differences occur between individuals in this regard but further work is necessary to elucidate the genetic mechanisms involved.

Haemoglobin

It has been shown that differences between individuals with respect to the type of haemoglobin in the erythrocytes, occur in several mammalian species. Such differences are genetically controlled. From electrophoretic analysis of quokka blood, Kirk has so far been unable to demonstrate haemoglobin differences between individuals of this species (unpublished data).

Erythrocyte Electrolytes

In most mammalian species, potassium is the predominant cation, sodium being present in only small concentrations. However, in carnivores sodium is the predominant cation in erythrocytes and in sheep, goats and possums, different individuals have either high sodium or high potassium erythrocytes.

Eadie (unpublished data) showed that quokka erythrocytes are unusual in containing roughly equal concentrations of sodium and potassium and that pouch young are not different from adults in this respect; J. Barker (unpublished data) confirmed this in studying the variation of erythrocyte sodium and potassium distribution between individual quokkas and is at present investigating other properties of these cells.

Endocrinology

Adrenal Physiology

The adrenal cortex produces hormones that are essential to life in a wide range of vertebrate species that have been investigated. When these animals are adrenalectomised, they die after varying periods of time (which are fairly characteristic for each species) during which they exhibit typical symptoms resulting from disruption of electrolyte, water and carbohydrate metabolism. However, the North American opossum, *Didelphis virginiana*, has been shown to be unusually resistant to adrenalectomy and there was thus the possibility that this might be a characteristic of the marsupial group. This hypothesis is not substantiated by the observations of Buttle, Kirk and Waring (1952) who reported that adrenalectomised quokkas have a short survival time (approximately two days) during which typical symptoms of adrenal in-

sufficiency, such as loss of appetite, muscular weakness, depression of blood glucose and plasma sodium levels and elevation of plasma potassium, occur.

Animals living under conditions of environmental stress are very dependent on their adrenal cortex secretions which aid the body cells to cope with the additional functional requirements imposed upon them by the stress conditions. In such situations, the rate of secretion of adrenal cortex hormones is increased above normal and if the stress is severe and/or prolonged the animals suffer from exhaustion of adrenal function. A concomitant effect with increased adrenal activity under conditions of stress is depression of the ascorbic acid content of the adrenal cortex. These facts were used by Herrick (unpublished data) in an investigation of variation of adrenal function in quokkas at different seasons, in relation to dehydration stress. Herrick's results indicated that there was an increase in adrenal cortex secretion in quokkas subjected experimentally to severe dehydration. However, he obtained no evidence of unusual adrenal activity or of dehydration in wild animals caught on Rottneest Island during summer or winter months.

The various investigations bearing on water metabolism which have been mentioned provide no evidence that dehydration stress is an important factor in population limitation among the quokkas on Rottneest Island (and see the report on Rottneest field studies in this part). It may, of course, account for death of a small number of animals which were not represented in the samples obtained by the various workers.

Reproduction

Valuable contributions to the field of comparative reproductive physiology have been made by extensive investigations of reproduction in the quokka, particularly since there is remarkably little information of this nature concerning the marsupial group.

Sharman (1954) commented on, and Waring, Sharman, Lovat and Kahan (1955) described the anatomy of the reproductive tract of the female quokka, which is similar in all important respects to that of other marsupials, and of the pouch, which contains four nipples, and recorded some observations on the birth and pouch life development of the young. Thus, the animals appear to be exclusively monovular, since multiple births have never been recorded. New born quokkas (which weigh approximately half a gram) move into the pouch and attach to one of the nipples which hypertrophies, along with the mammary gland that supplies it, as the foetus grows. Only the one nipple is used by any one young during lactation. The sexes are externally indistinguishable at birth and remain so for about three weeks after which either pouch or scrotum can be distinguished. The young are born in an undeveloped condition, but by the time they are about five months old, their eyes are open and they are well covered with fur. They remain permanently in the pouch for a total period of about six months after which they leave it for increasing periods of time until they are finally too large to enter it. Even though no longer resident in the

pouch, they continue to feed from the elongate nipple which often protrudes from the pouch, until they are about 9-10 months old.

Sharman (1955a) studied the oestrus cycle of the adult female quokka. He observed that the non-breeding part of the year (period of anoestrus) for quokkas in the wild lasts approximately from October to January. Towards the end of January, the breeding season starts with the commencement of oestrus cycles—these animals are polyoestrus within the breeding season. As in many other species, domestication results in reduction and finally elimination of the anoestrus period, in which case oestrus cycles recur throughout the year and are only interrupted by pregnancy and lactation. Each oestrus cycle is about 28 days in length. The period of behavioural oestrus in each cycle lasts for about 12 hours and is followed, within the next 24 hours, by ovulation, whether or not copulation has occurred. Details of the changes in the ovaries, uterus and vagina during the oestrus cycle and the anoestrus period are given and similarities between the cyclical changes in the female quokka and those in *Didelphis*, *Bettongia* and *Dasyurus*, the only other marsupials for which detailed information is available, are described.

Details of pregnancy and embryonic development of the quokka were described by Sharman (1955b). This account shows that the quokka placenta is of the yolk sac type and that the gestation period is about 26 days. After parturition, the female develops an oestrus condition and ovulation occurs: copulation and fertilisation of the post partum ovum may occur at this stage, but development of this zygote normally proceeds only to the blastocyst stage. While the first young remains in the pouch, the blastocyst stays in a quiescent state, unimplanted in the uterus which remains in an undeveloped state of lactation anoestrus. If the pouch-young is removed, the blastocyst becomes implanted and starts to develop further, the uterus changes to the pregnant condition and a second young is eventually born.

This mechanism would account for the fact that *domesticated* female quokkas have occasionally been observed feeding two young at the one time—one no longer resident in the pouch, but still feeding from the exterior by the elongate nipple to which it was previously attached, and the other newly born and attached to a different nipple. In such a case, the blastocyst would have remained viable for at least five months. However, this mechanism of delayed birth is probably of value in the wild population on Rottneest Island only in cases where the first young of the season is, for some reason, lost during earlier pouch life. By the time the first young normally leaves the pouch, seasonal anoestrus would, in most cases, have commenced in the wild carrying female and under these conditions the quiescent blastocyst degenerates.

Nerve Physiology

Studies are in progress by Collin on the conduction velocity in nerves from quokkas of different size, in order to obtain data on the developmental aspect of nerve conduction.